

OBSERVATIONS ON THE RESPIRATION OF THE SABELLID POLYCHAETE SCHIZOBRANCHIA INSIGNIS

R. PHILLIPS DALES

Bedford College, University of London, London N.W. 1

Schizobranchia insignis Bush lives in tough fibrous tubes, mostly 10–20 cm. long and 5–10 mm. in diameter, attached to the underside of floating wharves, to pilings and to rocks on the Pacific northwest coast of America (Fig. 1, A). It may also be dredged from muddy bottoms.

The dense crown of orange, purple or grey branched filaments, which is used both for feeding and for respiration, may be expanded beyond the opening of the tube for long periods when the worm is undisturbed. For shorter periods the worm lies wholly within the tube. Worms also irrigate their tubes by waves of muscular contraction of the body wall which may pass in either direction. Irrigation occurs when the crown is expanded as well as when the worm is retracted within the tube.

That the crown of all sabellids is used for feeding may readily be confirmed by simple observation, but its importance in respiration appears to vary from one species to another. Zoond (1931) found a 63% fall in oxygen uptake after amputation of the crown in *Bispira volutacornis* (Montagu) and Fox (1938) found the same decrease when *Sabella spallanzanii* (Viviani) was similarly treated. On the other hand, Wells (1952) found that bisected *Sabella pavonina* Savigny showed no significant fall in total rate of oxygen uptake of the two parts, but that *Myxicola infundibulum* Rénier did, there being a sharp drop in total uptake when bisected, and the posterior part giving relatively lower values than those of *Sabella pavonina*. He concluded that in *Sabella*, while the current caused by the crown provides for the crown's own respiratory needs, it is the irrigation current which is of importance to the rest of the body. *Myxicola*, on the other hand, does not irrigate its tube and is wholly dependent on the crown which functions not only in feeding but as a gill.

These differences suggested that it might be of interest to investigate the activities of another sabellid under conditions as natural as possible. The importance of the crown in respiration has only hitherto been assessed by the drastic procedure of amputation, and the rate of oxygen uptake has never been measured with the rate of water transport through the crown. Consequently, I have made measurements of oxygen uptake by the worm when expanded and when wholly withdrawn within the tube. The volumes of water passed (1) through the tube and (2) through the crown have also been measured, and the percentage utilization of oxygen by the crown and by the remainder of the body estimated under normal circumstances. All measurements have been at 12–13° C.

All the observations were made on animals from wharves in the vicinity of Friday Harbor, Washington. I am glad of this opportunity to thank Dr. Robert L. Fernald and the Staff of the Friday Harbor Laboratories of the University of

Washington for their hospitality and help. I also wish to thank Professor H. Munro Fox, F.R.S., for helpful criticism of this paper.

Worms were stripped of their own tubes and accommodated in pieces of transparent plastic or transparent rubber tubing of suitable length and diameter. Such tubes reveal the activities of the worm, readily enable the tube to be linked to recording apparatus, and permit measurement of oxygen uptake under nearly

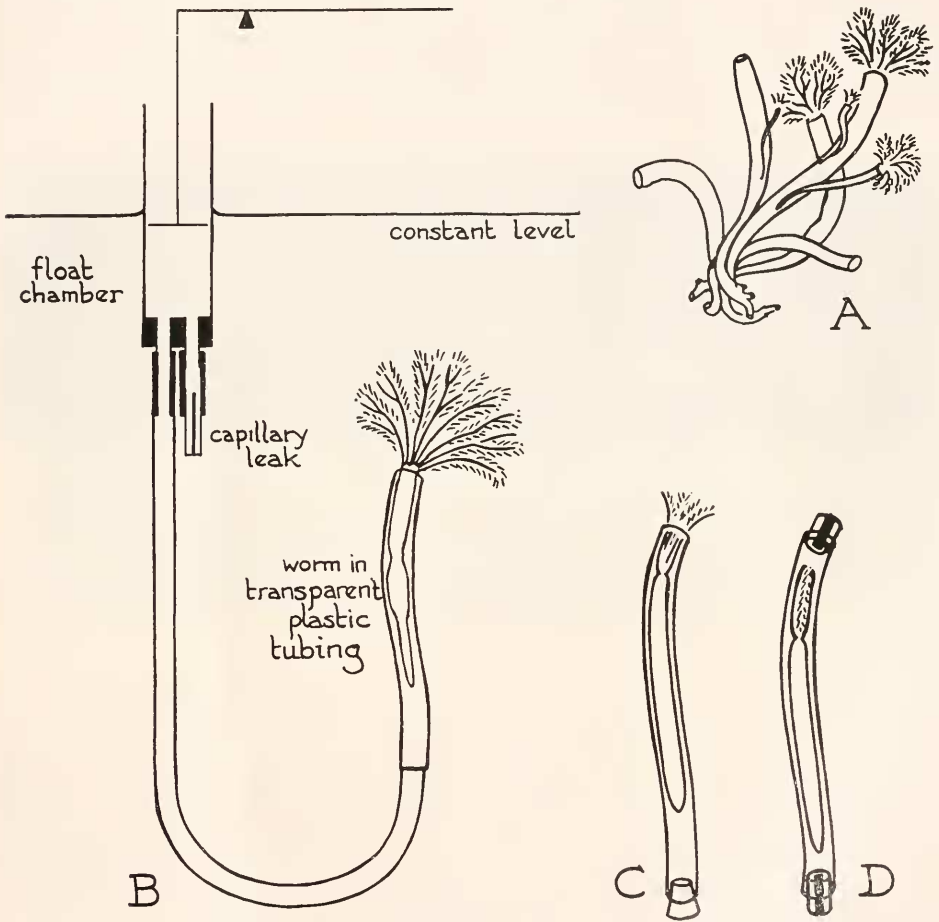


FIGURE 1. A, appearance of colony of *Schizobranchia* in nature; B, apparatus used to record irrigation; C, irrigation prevented; D, expansion prevented.

normal conditions. The work of Hyman (1932) and Fox (1938) emphasises the importance of simulating natural conditions as far as possible. Worms used in the experiments had been acclimatised to plastic or rubber tubes for at least one or two weeks.

EXTENSION AND WITHDRAWAL

To obtain some idea of the amount of time spent by the worm with the crown expanded, and the amount of time passed wholly withdrawn within the tube, worms

accommodated in plastic tubes were attached to a recording apparatus (Fig. 1, B) similar to that used by Wells (1951) for *Sabella*. The apparatus was immersed in a tank through which a circulation of sea water was maintained and in which the water level (1) remained constant. By adjusting the size of the capillary leak (a) the movement of the worm could be recorded on a slowly revolving kymograph by the lever actuated by changes in the level of the water in the float chamber (f). By selecting a larger capillary which allowed a more rapid flow than could be maintained by the worm irrigating under normal conditions, it was possible to adjust the capillary so that the float would be affected only by relatively rapid movements of the whole body, as in extension or withdrawal. Two typical traces, each of 12 hours duration, made by different worms are shown in Figure 2. It will

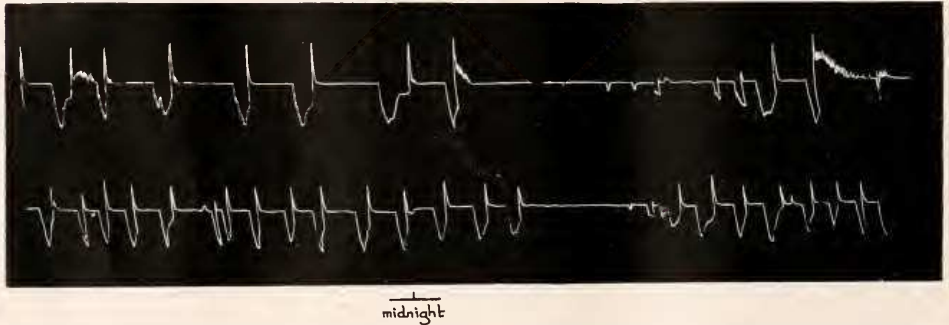


FIGURE 2. Continuous record of expansion and withdrawal by two different worms. Duration of each trace, 12 hours. Read from left to right. Upward spikes represent withdrawal within the tube, downward spikes represent extension from the tube with expansion of the crown. Extension is more gradual than withdrawal, as is shown by the stepped trace. The horizontal parts of the trace represent the times when the worm remained with the crown expanded beyond the opening of the tube.

be seen that extension and withdrawal occur at intervals of some regularity. The long period when the crown is expanded following extension after midnight was common to many worms and records. It may have been due merely to absence of stimulation by workers in the laboratory, although many other sabellids have been seen to expand their crowns more at night (McIntosh, 1922, Fox, 1938). It will be noticed that each period of expansion exceeded each period spent wholly withdrawn. The time spent retracted on any one occasion did not exceed 10–15 minutes, while periods of expansion were 20–60 minutes or longer. The interpretation of the records was confirmed by frequent observation.

IRRIGATION

Each tube, though firmly attached by mucus at or near the base to wharves or pilings, has one or more small openings 1 mm. or so in diameter near the hind end (Fig. 1, A). Mucus can be secreted through these to regain attachment, or new apertures made as occasion demands, and the orientation of the tube somewhat changed, as Fox (1938) observed in *Sabella spallanzanii*. Apart from these possibilities, which enable a small amount of re-orientation within the clump of animals so that each has room to expand the crown, *Schizobranchia* is completely sessile and

is unable to turn around in the tube except on its own longitudinal axis. Unlike *Sabella*, however, it rarely does so.

Irrigation of the tube is effected by muscular swellings passing down the body, most commonly from head to tail. Occasionally the direction of irrigation is reversed. These activities may occur when the crown is expanded or when the worm is withdrawn into the tube. The volume of the tube containing a worm of average size (2 grams fresh weight) is about 1.5 ml., the volume of such a tube empty being about 3.5 ml. Some idea of the irrigation rate may be obtained by injecting a suspension of carbon into the tube by means of a hypodermic syringe, and observing the rate of travel of the particles along a horizontally fixed graduated tube sealed on to the hind end. Under otherwise normal conditions the fluid in the tube may be completely renewed in 30–60 seconds of activity.

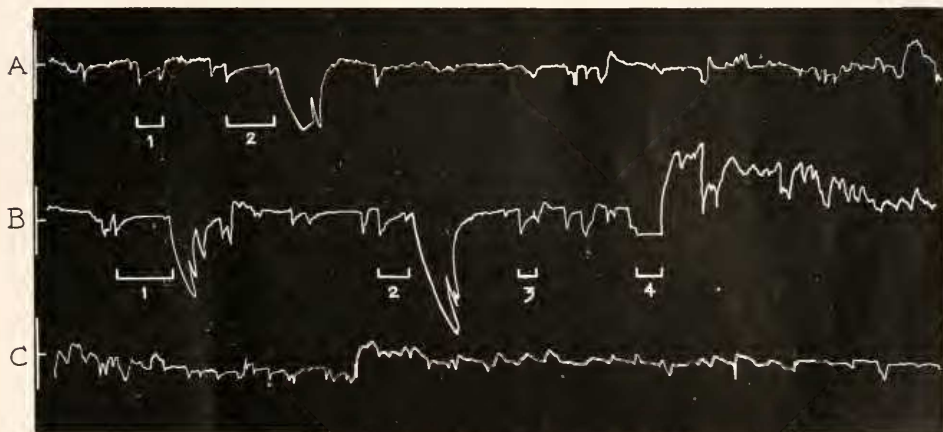


FIGURE 3. A–C, continuous record of irrigatory activity of a single worm over a period of 36 hours. Read from left to right. Each line represents 12 hours. Further explanation in text.

A continuous record of irrigation may be obtained with the apparatus already described by attaching a finer capillary at (a), such that the flow into or from the tank causes a slight rise or fall of 1–3 mm. to occur in the float chamber. A pressure difference of this magnitude may easily be recorded, but is unlikely to be great enough to modify the behaviour of the worm. A record of such activity is shown in Figure 3, C. The details of such traces were interpreted by watching worms from time to time while the trace was being made.

In the records elevation represents irrigation headwards; depression, tailwards. Irrigation will be seen to be somewhat irregular in rate, but to be fairly continuous. The volume passed can be calculated, knowing the dimensions of the capillary and the rest of the apparatus (Wells and Dales, 1951), or may be determined empirically. The average rate was found to be 0.3–0.5 ml./min. for a 2-gram (fresh weight) worm. Wells (1952) found a similar rate for *Sabella pavonina* of comparable weight. By inserting a small bung into the opening of a worm's tube attached to the recording apparatus, extension of the worm and irrigation could be stopped. If the period of closure did not exceed 10–15 minutes (Fig. 3, A: 1; Fig. 3, B: 3) normal activity was resumed after release. If this period was exceeded (20–45-

minute closure) as in Figure 3, A: 2; Figure 3, B: 1, 2, release was followed by very vigorous irrigation, as much as 0.75 ml./min. being passed for an hour or more by a 2-gram worm.

By connecting another piece of tubing to both the open end of a plastic tube in which a worm had been accommodated and attached to a recording apparatus (Fig. 1, B), and to the jet from the float chamber instead of the capillary leak, the circulation could be closed without preventing the worm from irrigating. Under

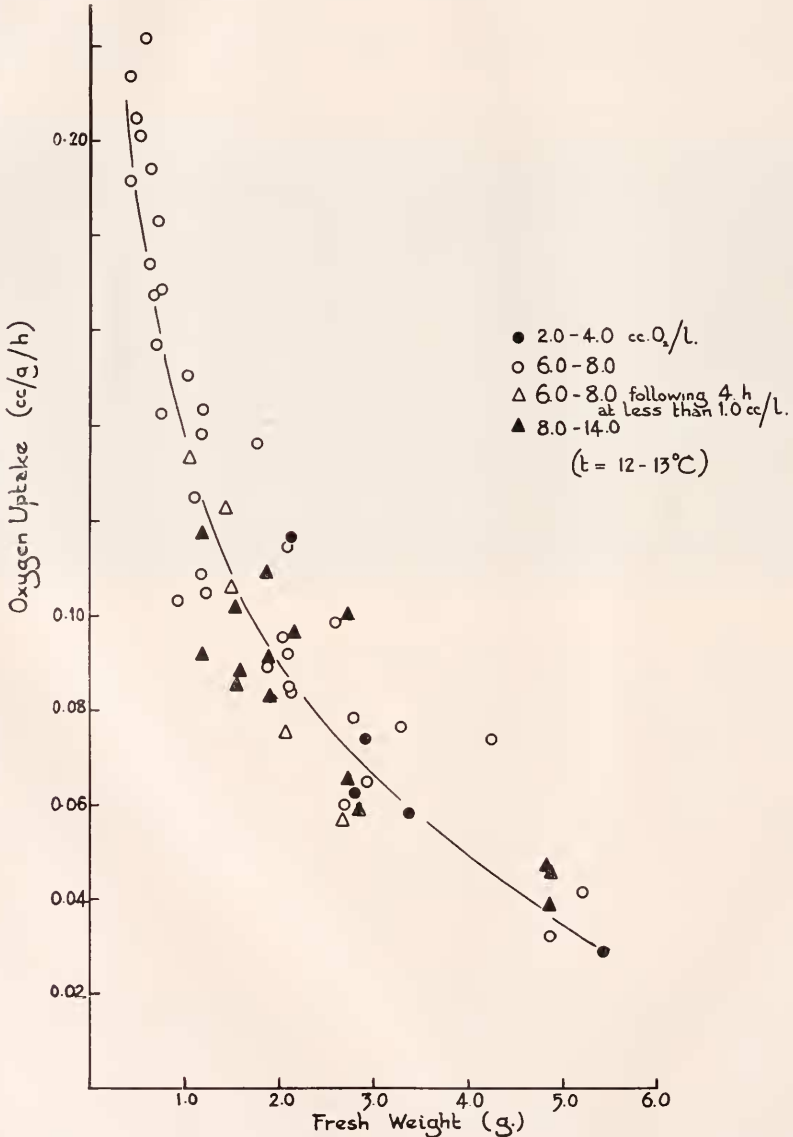


FIGURE 4. Rate of oxygen uptake under different external oxygen concentrations.

normal conditions worms underwent short bursts of "testing" activity, driving first in one direction and then in the other, and on release continued vigorous irrigation for some hours. Wells (1951) found that *Sabella spallanzanii* responded similarly. In Figure 3, B: 3, a burst of testing irrigation in a headward direction was in progress on release, and this direction was maintained for the following two hours, the worm gradually returning to its normal behaviour pattern.

OXYGEN UPTAKE

The rate of oxygen uptake was measured by the modification of Fox and Wingfield (1938) of the well-known Winkler technique. The rates of uptake made under different oxygen concentrations plotted against total fresh weight are presented in Figure 4.

Uptake was measured in closed bottles after a period long enough to ensure accurate estimation, but normally not so long that the quantity of oxygen in the bottle was reduced to not less than 4–5 cc./l. or the quantity of carbon dioxide increased to a level at which the rate might be affected. Bottles of approximately 270 ml. capacity were used and most measurements were made after a 1–4-hour period, according to the size of the animal. Worms thoroughly acclimatised to plastic tubing were used, as measurements so made might be expected to be closest to those under entirely natural conditions; Fox (1938) found that the oxygen uptake in *Sabella spallanzanii* was 20–30% lower in worms freshly deprived of their tubes. Each animal was therefore enclosed in a bottle large enough to ensure normal activity; worms were able to expand the crown, to withdraw and to irrigate. The bottles were occasionally inverted to ensure thorough mixing; most of the worms were acclimatised to being disturbed and their behaviour appeared to be affected only momentarily. All the determinations were made at 12–13° C.

(a) Response to raised or lowered oxygen content of the water

The normal rate of oxygen uptake could be maintained by the worm when the oxygen content of the water was lowered to 2 cc./l., either gradually by the animal itself over an extended period in a closed bottle, or by bubbling nitrogen through the water before the experiment. When the oxygen content was slowly reduced by the animal itself, the rate of uptake was significantly reduced between 1.3–2.5 cc. O₂/l.

If enclosed in a small chamber so that the rate of pulsation of the branchial vessels could be observed, the normal rate of 9–10 pulsations/min. (13° C.) fell off rapidly below about 2.5 cc. O₂/l., and ceased altogether around 1.3 cc. O₂/l. Fox (1938) found the same effect in *Sabella spallanzanii*.

The rate of oxygen uptake was not affected by raising the oxygen content of the water, similar values being obtained up to 14.0 cc. O₂/l. It is interesting, however, in confirmation of the findings of Fox and Taylor (1955), that worms were not adversely affected by these high concentrations, and survived indefinitely in the laboratory circulation which had a high oxygen content (7–8 cc. O₂/l.) owing partly to the action of the pumps. These sabellids are indeed usually found in habitats with a good circulation of water where the concentration of oxygen is likely to be high. Fox (1932) and Ewer and Fox (1940) have shown that the chlorocruorin of *Sabella spallanzanii* blood is adapted for oxygen transport only at

high outside concentrations, and C. Manwell (private communication) has found the same in *Schizobranhia insignis*.

(b) *Uptake of oxygen when extended*

When the crown was removed, and after the animal had recovered from the operation for a day or two, the oxygen uptake by the rest of the body was measured; the value obtained was about 25% that of the normal animal.

With normal animals irrigation, and hence normal respiratory exchange across the body wall, could be stopped by plugging the hind end of the tube (Fig. 1, C). Observation suggested that such worms remained extended more continuously, and measurement of oxygen uptake in closed bottles showed that the values obtained were not significantly different from those of normally irrigating worms. In other

TABLE I

Rate of oxygen uptake under normal conditions, when irrigation is prevented (as in Fig. 1, C), and when confined within the tube (as in Fig. 1, D)

Worm number	Total fresh weight	O ₂ uptake under normal conditions (cc. g./hr.)	O ₂ uptake without irrigation (Fig. 1, C)	O ₂ uptake under forced withdrawal (Fig. 1, D)
16	0.460	0.1920	0.1790	0.0782
17	0.520	0.2330	0.2266	0.0819
18	0.600	0.2210	0.2165	0.0759
19	1.205	0.1132	0.1568	0.0463
20	0.565	0.2212	0.2298	0.0696
21	0.765	0.1684	0.1851	0.0855
22	2.100	0.0916	0.1114	0.0316

words, normal oxygen uptake can be maintained by the crown alone (*i.e.*, without uptake through the body wall), though it may have to remain expanded to do so. Wells (1952) found that crownless *Sabella parvonia* perished if unable to irrigate.

(c) *Uptake of oxygen when withdrawn*

When withdrawn within the tube the crown is not well displayed for respiratory exchange or feeding, as the numerous branched filaments are tightly rolled together. By fitting a narrower tube to the opening (Fig. 1, D) extension could be prevented but irrigation continued. Under these conditions oxygen uptake was reduced, usually to about 40% of the normal value. On release, worms remained extended for some time. Values obtained for seven worms in which measurements of oxygen uptake were made under normal conditions, with irrigation prevented, and when wholly withdrawn, are compared in Table I.

RATE OF FILTERING BY THE CROWN

When the crown is extended water flows through the filaments as a result of ciliary activity. A measure of the volume of water strained through the crown may be obtained by the use of colloidal graphite suspensions, since the particles coming into surface contact are removed from suspension by mucus. Removal of particles is exponential if the system remains constant in volume and the particles

remaining in suspension are evenly distributed (Dales, 1957). Particles may be ingested or rejected, but in either case are removed from suspension. The rate at which unit volume is cleared of particles may be calculated by measuring the decrease in density at known intervals against controls (Jørgensen, 1949). The filtering rate in ten experiments was calculated over a three-hour period using worms of 0.5–2.0 grams fresh weight at 12–13° C. The mean rate of filtering was 70.7 ml./g./hr. This is of the same order of magnitude as has been found in other sabellids (Dales, 1957).

DISCUSSION

All these observations suggest that the life of *Schizobranhia insignis* is very similar to that of *Sabella spallanzanii*. Both species may be found in tubes open at the hind end attached to rocks and wharves. Both irrigate their tubes with equal facility in either direction, and pause in this activity for periods rarely exceeding 10 minutes.

It is difficult to assess the part played by the crown in supplying the respiratory needs of the rest of the body since, as Wells (1951, 1952) has pointed out, the needs of the crown itself are high owing to its activity. The vascular supply to the crown may be of service both in conveying oxygen away and in conveying nutrients to the ciliated epithelium and other tissues of the crown. The ability to continue to live, and to regenerate the crown when this is amputated, provided that the worm is able to irrigate its tube, suggests that the crown is not essential, although under normal circumstances it may well supply part of the body's needs.

Schizobranhia cannot autotomize the crown as *Sabella* does, so that decapitation results in a more serious loss in the total blood volume and perhaps a more unusual derangement of metabolism than in *Sabella*. While some individuals did regenerate their crowns, many died under laboratory conditions; *Sabella* seems better adapted for this contingency. The crown is also relatively larger in *Schizobranhia*, and the reduction in oxygen uptake to 25% of the normal value may well be partly due to the loss of that part of the uptake accounted for by the crown itself. When the worm is retained in the tube (or when, in nature, the worm is wholly withdrawn) the irrigation current alone supplies oxygen to the animal and removes carbon dioxide and other waste products. Under these conditions the oxygen uptake is 40% of that when extended. While the crown is not then expanded and the animal's need for oxygen may be somewhat less, the cilia on the crown do not cease to move, and the muscular contractions causing irrigation of course continue. It could be argued that if crownless worms can continue to live, providing that they are able to irrigate, and that the oxygen uptake of crownless worms is 25% of what it was before decapitation, then the requirement of oxygen for maintaining irrigation may be met by 25% of the normal total oxygen uptake. Other activities may well be interrupted after decapitation, but the major part of the remaining 75% of the normal oxygen uptake may thus be accounted for by the activity of the crown itself. That worms wholly withdrawn (Fig. 1, D) have an oxygen uptake of 40% of the value for expanded though not continuously irrigating worms (Fig. 1, C) suggests that perhaps a value approaching 60% of the total oxygen uptake is due to the activity of the crown alone. While the circulation of the blood from the crown can supply the respiratory needs of the rest of the body if irrigation is not possible, under normal circumstances it need not do so. Uptake

of oxygen will ensure, through the intermediacy of the vascular system, a supply of oxygen to all parts at all times, for activity of the crown and irrigation are independent activities.

Pulsation of the branchial vessels was observed by Fox (1938) and Wells (1951) in *Sabella* to cease after some time when totally enclosed in a small chamber or in a tube, and cessation may be seen also in *Schizobranchia*. As already noted, pulsations occur under normal circumstances at a rate of about 10/min. at 13° C., but these cease altogether when the oxygen content of the water has fallen to about 1.3 cc. O₂/l. Fox (1938) suggested that this effect may be due to accumulation of carbon dioxide, but as Wells (1951) points out, this is unlikely to occur under normal conditions owing to irrigation. On the other hand, if the worm is wholly withdrawn and, while ceasing to irrigate, its uptake of oxygen remains at 40% of its normal value (0.1 cc. O₂/hr. for a 2-gram worm), the oxygen contained in the 1.5 ml. of water within the tube would be used up in 15 minutes. The possibility that the factor which ends a short rest from irrigation might be lack of oxygen or accumulation of carbon dioxide should not, therefore, be dismissed. In *Schizobranchia*, however, pauses were never observed to be as long as this, and in any case when the irrigatory waves cease the oxygen requirement should be less. In addition, there should be sufficient oxygen in the blood to provide for such brief pauses as occur (Ewer and Fox, 1940) and it seems more likely from the work of Wells (1951, 1955) that the resumption of irrigation is spontaneous.

The measurement of filtration rate showed that 70 ml. of water/g./hr. was moved across the filaments by the activity of the crown cilia, while the normal irrigation rate through the tube was about 12 ml./g./hr. While it would be unwise to draw too close a comparison, these figures suggest that the crown is in fact achieving more effectual work in water transport than the body when irrigating, so that it is not surprising to find that the total oxygen uptake is reduced to 40% when the crown is not expanded. The utilization of oxygen from the water passed through the crown may be obtained from the filtration rate (70 ml./g./hr.) and the rate of oxygen uptake (0.05 cc. O₂/g./hr.). Under laboratory conditions (external oxygen content of 7.0 cc. O₂/l.) this can be estimated at about 10%. When the worm is wholly withdrawn the oxygen consumption falls, as we have just noted, to 40% of the normal value or 0.02 cc. O₂/g./hr., which is withdrawn from only 12 ml., giving a utilisation of about 24%. The rather low utilisation by the crown rather suggests that the flow is maintained more for feeding than for respiration.

Wells (1951) suggested that in *Sabella pavonina* feeding was at least a possibility when the crown is withdrawn. While this may be so in *S. pavonina*, which has a singularly delicate and "open" crown, it seems far less likely to occur in *Schizobranchia* in which the crown is more complicated, much branched, and closely furled when contracted.

The results discussed here suggest that *Schizobranchia* is able to maintain its respiratory needs when withdrawn within the tube, and that it emerges to feed in response to some spontaneous mechanism such as Wells (1955) has described in other polychaetes. This ability to meet the demand for oxygen by irrigation when withdrawn within the tube is a factor with obvious survival value. It is interesting that sabellids such as *Myxicola* (Wells, 1952) and *Chone*, which do not irrigate their tubes, have exceptionally well developed giant fibre systems and retraction responses. This should increase their chances of survival, for not only are these

worms dependent on their crowns for respiratory exchange but the crowns must, therefore, be more constantly displayed.

SUMMARY

1. Observations on the life of a sabellid *Schizobranchia insignis* have been made under conditions resembling as far as possible those found in nature.

2. The amount of time spent with the crown expanded and the amount passed wholly withdrawn within the tube have been measured, and the utilisation of oxygen under these two conditions estimated.

3. The volume of water passed through the crown for respiratory and feeding purposes, as well as the volume pumped through the tube, have also been measured, and the part played by each in respiratory exchange discussed. It was found that about 70 ml./hr./g. animal (fresh weight) is passed through the crown by the action of the filamentary cilia, and the volume pumped through the tube is about 12 ml./hr./g.

4. Utilisation of oxygen by the crown is relatively low (10%); utilisation by the whole worm when withdrawn is about 24%, and the large volume strained by the crown is probably related to the food requirements rather than to the respiratory needs of the worm.

5. It is suggested that the oxygen taken up by the crown is largely utilised in its own activity although it can, and does, provide for the needs of the rest of the body during pauses in irrigation when expanded.

LITERATURE CITED

- DALES, R. P., 1957. Some quantitative aspects of feeding in sabellid and serpulid fan worms. *J. Mar. Biol. Assoc.*, **36**: 309-316.
- EWER, R. F., AND H. M. FOX, 1940. On the function of chlorocruorin. *Proc. Roy. Soc. London, Ser. B*, **129**: 137-153.
- FOX, H. M., 1932. The oxygen affinity of chlorocruorin. *Proc. Roy. Soc. London, Ser. B*, **111**: 356-363.
- FOX, H. M., 1938. On the blood circulation and metabolism of sabellids. *Proc. Roy. Soc. London, Ser. B*, **125**: 554-569.
- FOX, H. M., AND A. E. R. TAYLOR, 1955. The tolerance of oxygen by aquatic invertebrates. *Proc. Roy. Soc. London, Ser. B*, **143**: 214-225.
- FOX, H. M., AND C. A. WINGFIELD, 1938. A portable apparatus for the determination of oxygen dissolved in a small volume of water. *J. Exp. Biol.*, **15**: 437-445.
- HYMAN, L. H., 1932. Relation of oxygen tension to oxygen consumption in *Nereis virens*. *J. Exp. Zool.*, **61**: 209-221.
- JØRGENSEN, C. B., 1949. The rate of feeding by *Mytilus* in different kinds of suspension. *J. Mar. Biol. Assoc.*, **28**: 333-344.
- MCINTOSH, W. C., 1922. A Monograph of the British Marine Annelids, **4**, London (Ray Soc.).
- WELLS, G. P., 1950. Spontaneous activity cycles in polychaete worms. *J. Exp. Biol. Symposium II. Physiological mechanisms in animal behaviour*: 127-142.
- WELLS, G. P., 1951. On the behaviour of *Sabella*. *Proc. Roy. Soc. London, Ser. B*, **138**: 278-299.
- WELLS, G. P., 1952. The respiratory significance of the crown in the polychaete worms *Sabella* and *Myricola*. *Proc. Roy. Soc. London, Ser. B*, **140**: 70-82.
- WELLS, G. P., AND R. P. DALES, 1951. Spontaneous activity patterns in animal behaviour: the irrigation of the burrow in the polychaetes *Chaetopterus variopectatus* Rénier and *Nereis diversicolor* O. F. Müller. *J. Mar. Biol. Assoc.*, **29**: 661-680.
- ZOOND, A., 1931. Studies in the localization of respiratory exchange in invertebrates. II. The branchial filaments of the sabellid, *Bispira voluticornis*. *J. Exp. Biol.*, **8**: 258-266.